Habitat Differences Among Container-Breeding Mosquitoes in Western Puerto Rico (Diptera: Culicidae)

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Aedes aegypti (Linn.), the vector of dengue virus in the Caribbean, has assumed major importance in recent years because of continued dengue epidemics (Neff *et al.*, 1967; Likosky *et al.*, 1973; Von Allmen *et al.*, 1979).

From 1964 to 1968, an intensive *Ae. aegypti* Eradication Program was carried out in the southeastern United States, Puerto Rico, and U.S. Virgin Islands. During that program, there was widespread removal of container habitats in the domestic and peridomestic environment and insecticidal treatment of remaining habitats. McClelland (1967) suggested that this type of treatment might profoundly affect the behavior of a "weedy" species, such as *Ae. aegypti*, by applying strong selective pressure to change breeding site selection. Intensive control would eliminate panmictic breeding, leading to higher inbreeding rates, which would further enhance rapid evolutionary change. According to McClelland (1967), any repellent quality of the insecticides used to treat larval habitats would also increase selection by inducing ovipositing females to seek untreated containers, presumably those not considered the usual types or those at some distance from houses. Moore (1977) subsequently found that Abate®[2] and malathion, two widely used larvicides, repelled ovipositing *Ae. aegypti.*

Kellett and Omardeen (1957) found *Ae. aegypti* in Trinidad breeding in tree holes as high as 10 meters above ground level. They suggested this behavior might be related to repellent action of benzene hexachloride (BHC) used for larval control. Fox *et al.* (1960) found *Ae. aegypti* breeding in coraline rock holes in western Puerto Rico. Larvae from rock holes were found to be highly resistant to DDT, dieldrin, and lindane. Weinbren and O'Gower (1966) and Weinbren and Weinbren (1970) reported *Ae. aegypti* breeding in the Luquillo rain forest in eastern Puerto Rico. However, Haber and Moore (1973) concluded that the rain forest infestation resulted from introduction of eggs during a long-term radiation ecology experiment, and no evidence of permanent establishment was found.

The foregoing reports of habitat and behavior changes prompted a survey of *Ae. aegypti* distribution with respect to container habitat and distance from houses in western Puerto Rico. The study also provided an opportunity to evaluate possible competition between *Ae. aegypti* and the local *Ae. (Gymnometopa) mediovittatus (Coq.)* and to assess the degree of association between the various container-breeding mosquito species.

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[2] Use of trade names is for identification only and does not constitute endorsement by the Public Health Service or by the U.S. Department of Health and Human Services.
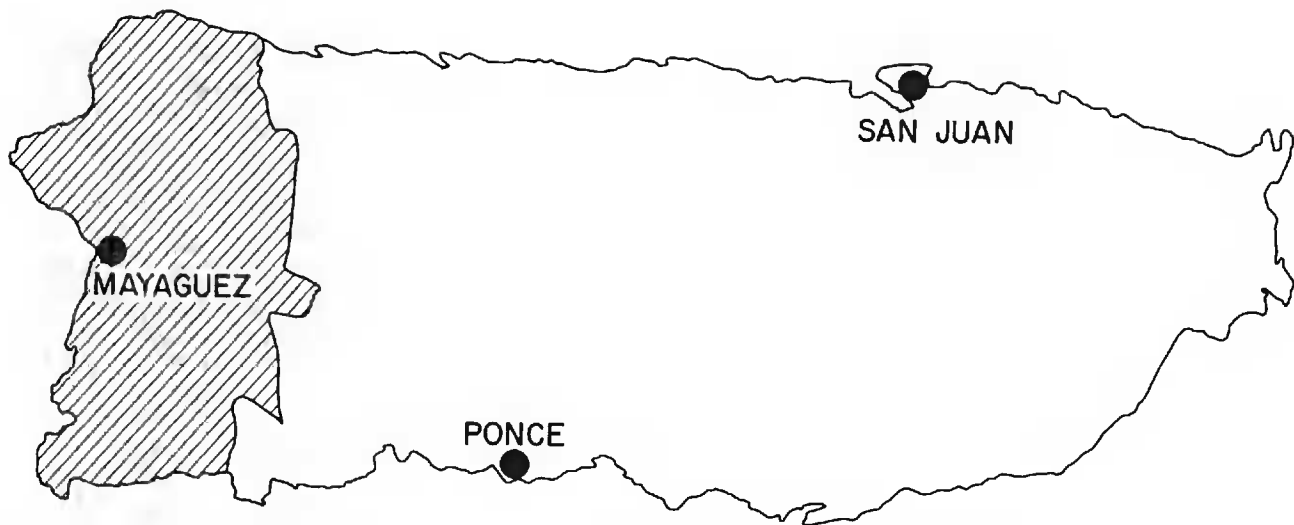
Fig. 1. Location of study area in Puerto Rico. Municipalities surveyed were Aguada, Aguadilla, Añasco, Cabo Rojo, Hormigueros, Isabela, Lajas, Las Marias, Maricao, Mayaguez, Moca, Rincon, Sabana Grande, San German, and San Sebastian.

Materials and Methods

This study was carried out concurrently with collections of local mosquito species for the "Mosquitoes of Middle America" (MMA) project (Belkin *et al.,* 1965a, b). Egg, larval, pupal, and adult mosquito collections were made from artificial (man-made) and natural (e.g., tree holes, rock holes, plant axils) water-holding containers or holes around rural dwellings in 15 municipalities in western Puerto Rico (Fig. 1), from January through June, 1971. Collecting methods were as described by Belkin *et al.* (1965b), and collection data were recorded on the standardized MMA collection form. Distance from the nearest house was also estimated and noted on the collection form. Collections were returned to the laboratory for identification. Scrapings and other collections of dried material were flooded with water and subjected to vacuum for 15 to 30 minutes to induce hatching. Samples that did not produce larvae were dried and then flooded a second time. Samples producing no larvae after the second flooding were considered to be negative.

Larvae were reared in enamel pans (18 × 30 × 5 cm) containing approximately 1 liter of 0.01 M NaCl solution in place of tap water and were fed finely ground rabbit food. Larvae were identified in the fourth instar and, when appropriate, samples were preserved for the MMA project. When less common species were collected, individual rearings were carried out to preserve larval and pupal skins with the associated adults (Belkin *et al.,* 1965b). Representative samples of the material collected were deposited in the MMA project collection (Belkin and Heinemann, 1975), which is now located at the Smithsonian Institution.

Habitats were grouped by type and distance from the nearest human habitation. Container habitats were grouped according to source (artificial or natural) and size. Later, several groups were pooled to obtain reasonable sample sizes. The final categories were: 1) artificial containers—a) containers of 20-liter capacity or greater and b) containers of less than 20-liter capacity, and 2) natural containers of all sizes. The number of containers decreased as distance from houses increased. Most houses were grouped together and not separated from other houses by great distances; also, inspectors were less likely to discover all containers farther away

Table 1. Availability of distance data, type of sample and positivity of samples for 772 artificial and natural container habitats in western Puerto Rico, January–June 1971.

	Type of sample		Total
	Larvae/pupae	Scrapings	
Positive samples			
Distance known	383	8	391
Distance unknown	209	12	221
Total	592	20	612
Negative samples			
Distance known	2	79	81
Distance unknown	3	76	79
Total	5	155	160
Total samples	597	175	772

from houses. Thus, there was a highly skewed distribution of containers over distance from houses. To obtain a small number of distance classes with approximately equal numbers of collections, a logarithmic scale using four distance classes was based upon a 13X expansion, beginning at 0.5 (–1.70, 0.81, 1.93, . . . on the logarithmic scale) (Williams, 1964).

Data for species pairs were tested for positive or negative association by chi-square or Fisher's exact test and by calculation of Cole's (1949) coefficient of interspecific association (C_7), as described by Southwood (1966). Temperature and rainfall data were obtained from 19 weather stations scattered throughout the study area (NOAA, 1972). Changes in mosquito abundance during the study were examined for possible correlation with temperature and rainfall variations.

RESULTS

Twelve species of mosquitoes were collected during the study: *Aedes aegypti* (Linnaeus), *Ae. mediovittatus* (Coquillett),[3] *Anopheles grabhamii* Theobald, *Culex antillummagnorum* Dyar, *Cx. atratus* Theobald, *Cx. habilitator* Dyar & Knab, *Cx. nigripalpus* Theobald, *Cx. p. quinquefasciatus* Say,[4] *Cx. secutor* Theobald, *Toxorhynchites portoricensis* (Roeder), *Uranotaenia socialis* Theobald, and *Wyeomyia* sp. In addition, a chaoborid gnat (Diptera, Chaoboridae) was collected in rock hole habitats. Both the *Wyeomyia* and *Corethrella* spp. are apparently undescribed species (Belkin and Heinemann, 1975). Because the larval stages of chaoborids and culicids are morphologically and ecologically similar, the chaoborids are included within the Culicidae following Belkin *et al.* (1970).

Table 1 shows the number of positive and negative samples of different types. It was not always possible to determine distance to the nearest house, so that distance information was available for only 61% of the collections. Nearly all (97%) of the negative samples were scrapings from dry container habitats, mostly tree and rock holes. All negative samples were discarded from the analysis, since

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[3] Generic abbreviations for Culicidae follow Reinert (1975); *Co.* = *Corethrella*.

[4] Sirivanakarn (1976) elevated *Cx. p. quinquefasciatus* to full specific status. I have elected to retain the subspecific designation for this taxon because elevation only serves to further confuse an already complex biosystematic problem.
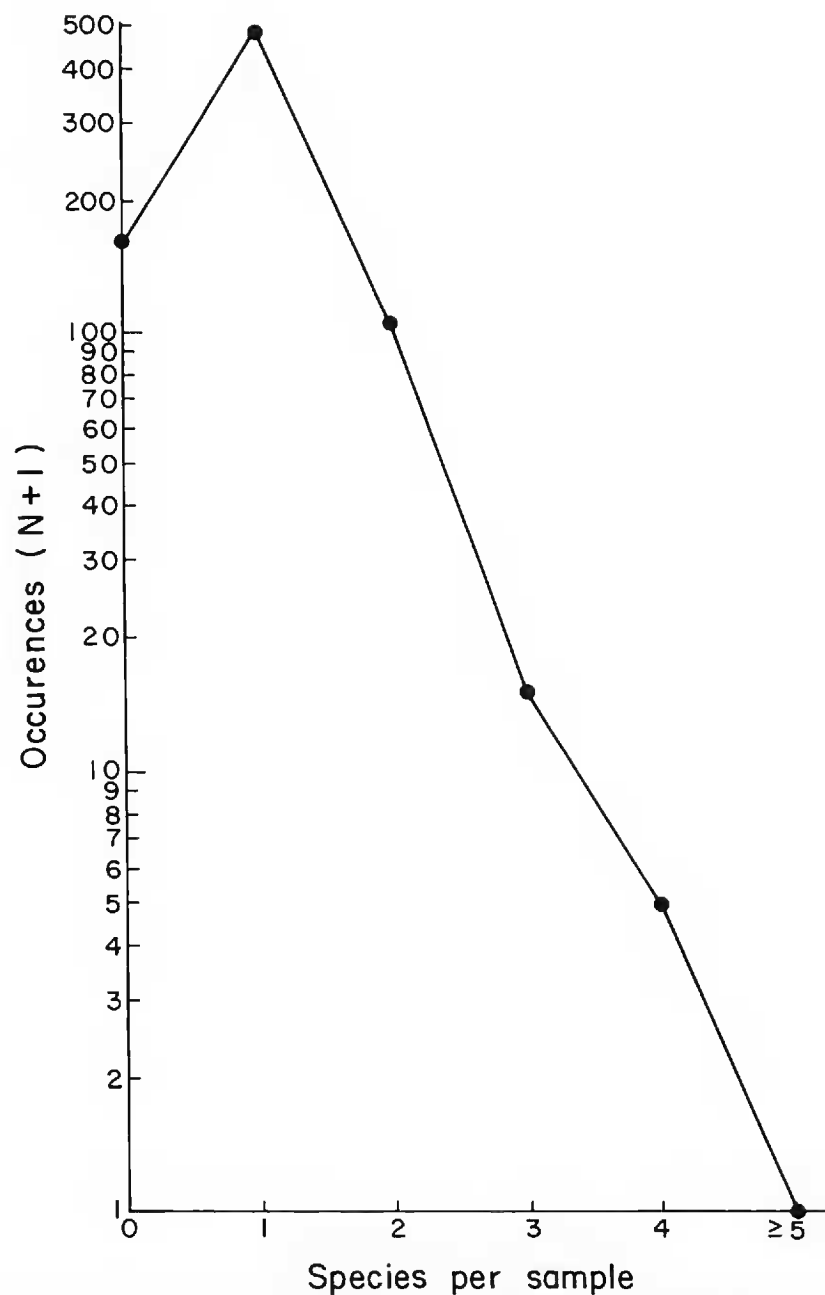
Fig. 2.   Number of species per sample in 772 collections from various artificial and natural water-holding containers, western Puerto Rico, January–June 1971.

true negativity (absence of viable mosquito eggs) could not be differentiated from methodological problems in the hatching technique.

Distance from human habitation and species per sample.—Of the 160 negative samples, 155 were collections of material removed from dry containers while 5 were collections of water thought to contain larvae or pupae. Of 612 positive samples, 488 (79.7%) contained a single mosquito species, 106 (17.3%) contained 2, 14 (2.3%) contained 3, and 4 (0.7%) contained 4 species (Fig. 2). No sample contained more than 4 mosquito species.

The number of species per sample was related to proximity to houses. In the 383 positive larval/pupal collections of known distance, single species collections were more frequent near houses, while multi-species collections were more frequent away from houses. The relationship was significant ($P < 0.05$, chi-square), regardless of the geometric class intervals (i.e., 3×, 5×, 11×, 13×, 17×, 23×) used to group the collections (Williams, 1964).

Collections from containers less than 1 meter from houses (i.e., inside, attached to, or resting against the house) accounted for 34% of all positive collections. Over 50% of all positive collections were made within 4 meters of a house, and 96%

Table 2.   Percent distribution of seven container-breeding mosquito species in relation to distance to nearest human residence, Puerto Rico ($n = 383$ samples).

Species	Distance from houses (meters)				Total samples
	<1	1–6	7–84	85–1098	
Ae. aegypti	44.0	37.0	18.1	0.8	243
Ae. mediovittatus	14.8	13.6	51.1	20.5	88
Co. sp.	0.0	10.7	42.9	46.4	28
Cx. antillummagnorum	6.7	26.7	33.3	33.3	15
Cx. p. quinquefasciatus	30.8	19.2	50.0	0.0	26
Cx. secutor	48.7	10.3	35.9	5.1	39
Tx. portoricensis	9.1	18.2	63.6	9.1	11
Samples per class	132	105	115	31	383

were no farther than 120 meters away from a house. In the areas under study, there were relatively few localities where houses were more than 240 meters apart.

Table 2 shows the distribution of the 7 most common species with respect to distance from houses. *Aedes aegypti* was most common near houses. *Aedes mediovittatus* was more common in collections away from houses, but nearly 30% of collections of this species were within 6 meters of a house. *Culex p. quinquefasciatus* and *Cx. secutor,* which share fairly similar container habitats, were somewhat similar in spatial distribution.

Importance of different kinds of container habitat.—Table 3 shows the relative importance of major container categories as breeding sites for the 7 most common mosquito species. Natural container habitats made up 23.8% (140/592) of all positive larval/pupal collections. Of those, 51.4% were rock holes, 32.1% were leaf axils, 7.1% were tree holes, and 9.3% were miscellaneous container types (snail shell, coconut shell, palm spathe, etc.). Because of the small numbers of collections from each container type, it was not possible to analyze the preference of a given species for specific kinds of natural containers.

Several species (e.g., *Ae. aegypti, Ae. mediovittatus, Cx. p. quinquefasciatus, Cx. secutor*) were broadly scattered among the different categories, while others (*Corethrella* sp., *Cx. antillummagnorum*) were highly selective and occurred only in a few kinds of container habitats. Several collections, such as *Cx. antillummagnorum* from rock holes, may be due to larvae being washed from a more common habitat into another habitat by heavy rain.

Culex secutor is primarily an inhabitant of pools in mountain streams (Belkin *et al.,* 1970), but as shown by these data, it has a broad range of larval habitats. It is also possible that the *Cx. secutor* of Puerto Rico consists of more than one species (Belkin *et al.,* 1970).

Zavortink (1972) recorded *Ae. mediovittatus* from all of the larval habitats shown in Table 3, plus ground pools, which were not sampled in this study.

The rock hole area previously studied by Fox *et al.* (1960) was located through the assistance of Mr. A. H. Boike. *Aedes aegypti* was still found breeding in the rock holes 12 years after their original survey. The rock hole area is located, as noted by Fox *et al.,* about 25 to 90 meters (80 to 300 ft) from the nearest houses. The area had been used as an unauthorized dump for some years, and by 1971, large numbers of artificial containers were present to serve as additional breeding

Table 3. Percent of breeding of 7 mosquito species in different container types, western Puerto Rico, 1971 ($n = 592$ samples positive for one or more species, adjusted for differing numbers of containers within types).

Species	Drum	Tire	Misc. ≥20 liters	Misc. <20 liters	Rock hole	Misc. natural
Ae. aegypti	29.7	22.7	13.0	17.7	7.8	9.1
Ae. mediovittatus	4.9	14.7	18.9	13.3	37.1	11.0
Co. sp.	0.0	2.2	8.2	3.1	86.5	0.0
Cx. antillummagnorum	0.0	4.1	7.1	10.3	5.0	73.4
Cx. p. quinquefasciatus	10.5	19.7	43.8	14.9	8.8	2.3
Cx. secutor	9.7	14.4	28.2	22.8	13.3	11.6
Tx. portoricensis	2.6	29.6	17.2	18.9	0.0	31.8
Total containers	178	87	50	137	72	68

sites. Fox *et al.* (1960) concluded that rock hole specimens of *Ae. aegypti* represented the spillover of oviposition due to population increases in other, more normal habitats, and no evidence was found in the present study to suggest otherwise. Additional coraline rock hole breeding sites were found near the town of Lajas.

Interspecific association.—Seven species were collected in sufficient numbers to permit calculation of Cole's (1949) coefficient of interspecific association (C_7). *Aedes aegypti* was negatively associated with all of the other 6 species (Table 4). *Aedes mediovittatus* was positively associated with *Corethrella* sp. All other species pairings were random (i.e., species were not associated).

Sufficient data were available for *Ae. aegypti* and *Ae. mediovittatus* to compute C_7's for either container type or distance from houses and, to a certain extent, for both factors simultaneously. There was a strong negative association between the species in terms of the type of container in which they occurred (Table 5). Table 3 shows the major differences in types of containers utilized. Water storage drums and tires were the most frequent sources of *Ae. aegypti*, while rock holes and miscellaneous large containers were the most frequent sources of *Ae. mediovittatus*. Joint occurrences of *Ae. aegypti* and *Ae. mediovittatus* were random with respect to distance from houses at 1–6 meters and 85–1098 m, but C_7's were significantly negative at distances of less than 1 meter and from 7–84 meters (Table 5). Only 28 percent of all *Ae. mediovittatus* collections occurred within 6 meters of a house, while 81% of all *Ae. aegypti* were found within that distance (Table 3). Lack of significance in C_7's at 1–6 and 85–1098 meters may have been due to small numbers of one species in these two distance categories, or even a zone of overlap in the 1- to 6-meter distance class.

Aedes aegypti and *Cx. p. quinquefasciatus*, both widely distributed domestic species, were negatively associated. The separation in this case appeared to be due to type of container and not to distance from houses. Most *Cx. p. quinquefasciatus* were found in tires and miscellaneous large containers (Table 4). Different preference for organic content of the container habitat probably also limits cohabitation.

Aedes mediovittatus and *Corethrella* sp., a predator, were positively associated ($C_7 = 0.40 \pm 0.10$, Table 4), and *Ae. mediovittatus* may form a major part of the

Table 4. Coefficients of interspecific association (C_7, Cole, 1949) between container-breeding mosquitoes in western Puerto Rico ($n = 383$ samples). $C_7 \pm$ SE significant (chi-square or Fisher's exact test) at $P \le 0.05$ (*), 0.01 (**), or 0.001 (***). NS = non-significant (random) association between species.

	Ae. mediovittatus	Co. sp.	Cx. antillum-magnorum	Cx. p. quinque-fasciatus	Cx. secutor	Tx. portoricensis
Ae. aegypti	−.71 ± .07***	−.89 ± .14***	−.89 ± .19***	−.48 ± .14**	−.68 ± .12***	−.71 ± .22**
Ae. mediovittatus	—	.40 ± .10***	−.13 ± .46 NS	−.03 ± .34 NS	.10 ± .08 NS	−.60 ± .54 NS
Co. sp.	—	—	−1.00 ± .90 NS	−.49 ± .66 NS	−.65 ± .54 NS	−1.00 ± 1.06 NS
Cx. antillummagnorum	—	—	—	−.05 ± .92 NS	−1.00 ± .75 NS	−1.00 ± 1.47 NS
Cx. p. quinquefasciatus	—	—	—	—	−.27 ± .55 NS	−1.00 ± 1.08 NS
Cx. secutor	—	—	—	—	—	.09 ± .10 NS

Table 5. Effect of container type and distance from houses on coefficient of association (C_7) between Ae. aegypti and Ae. mediovittatus in western Puerto Rico ($n = 383$ samples). $C_7 \pm$ SE significant (chi-square or Fisher's exact test) at $P \le 0.05$ (*), 0.01 (**), or 0.001 (***). NS = non-significant (random) association.

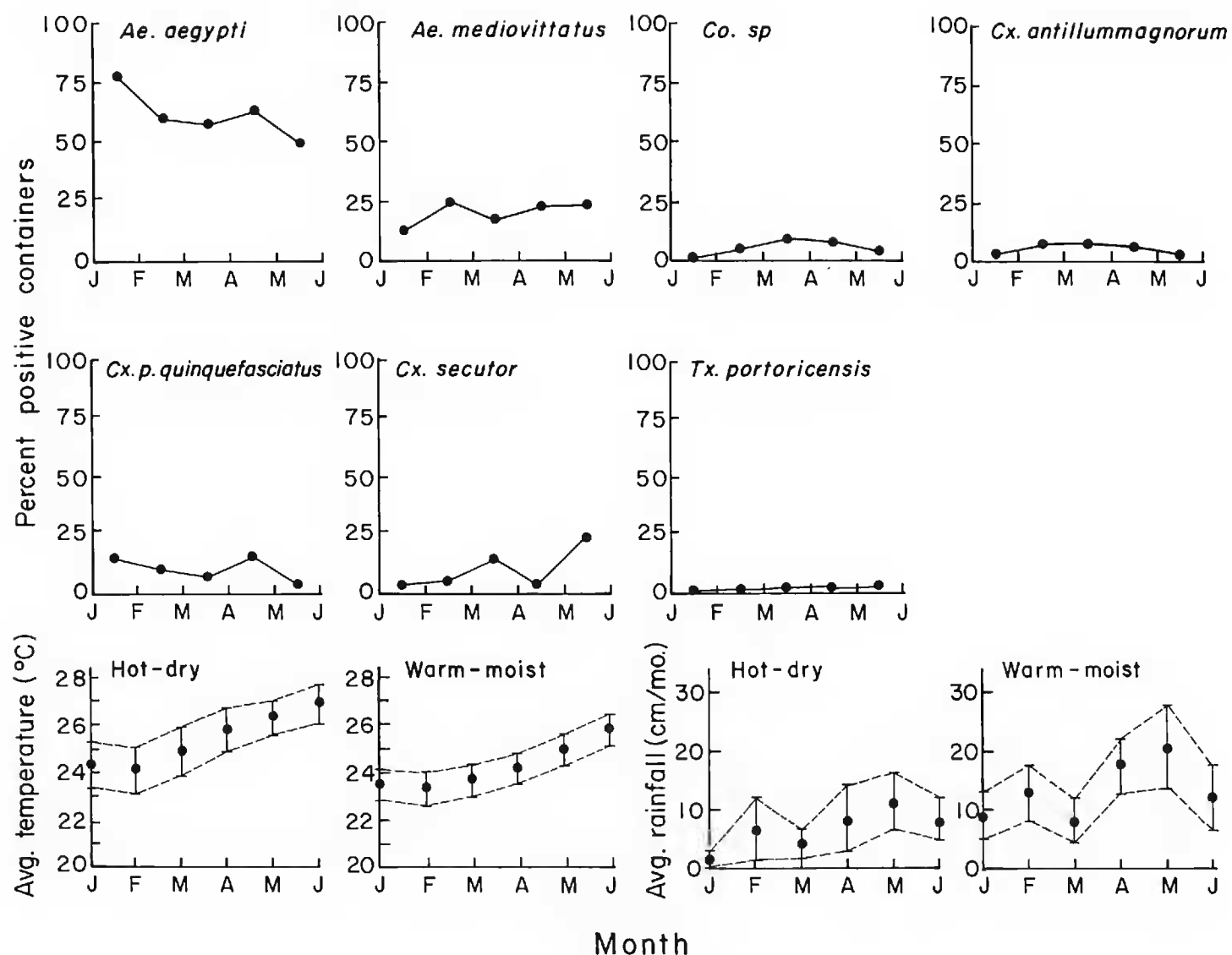| Container type	Distance (m)				All distances
	<1	1–6	7–84	85–1098	
Large, artificial	−.62 ± .12***	1.00 ± 2.30 NS	−1.00 ± .40*	−1.00 ± .41 NS	−.66 ± .08***
Small, artificial	−.63 ± .32 NS	−.40 ± .16*	−.69 ± .26*	—	−.61 ± .15***
Natural	—	−.23 ± .49 NS	−.76 ± .20***	—	−.78 ± .17***
All containers	−.62 ± .13***	−.22 ± .11 NS	−.77 ± .15**	−1.00 ± .58 NS	−.71 ± .07***

Fig. 3. Temperature, rainfall, and monthly abundance of container-breeding mosquito species in western Puerto Rico, January–June 1971 ($\bar{X} \pm$ SD shown for temperature and rainfall).

predator's diet. Moore and Haber (unpublished data) found that late instars of this *Corethrella* sp. consumed as many as 2.2 *Ae. mediovittatus* larvae per 24 h in laboratory experiments.

Weather pattern and temporal relationships between species.—The study area was not homogeneous with respect to temperature and rainfall. Average (January through June 1971) monthly temperature and rainfall for 11 stations in the study area fell into 4 distinct zones: a) hot-dry (26°C, 7 cm rain/month), b) warm-moist (24°C, 14 cm/month), c) cool-moist (21°C, 16 cm/month), and d) warm-wet (24°C, 21 cm/month). Approximately 95% of all collections came from the hot-dry or warm-moist zones.

January and February were the coolest months, and temperatures rose gradually and uniformly from March through June, when the study ended (Fig. 3). Rainfall was lowest in January. As is usual for the western part of Puerto Rico (Calvesbert, 1970), rainfall increased in February but was diminished again in March. Rainfall increased in April and May but was unusually low in June. June precipitation records were from 5 to 11 cm below normal for most parts of the island.

Some of the observed negative associations could have been due to temporal separation of population peaks, even though the study encompassed only a 6-month period (Fig. 3). Except for *Ae. aegypti* and *Cx. secutor,* the temporal occurrence of the species was fairly constant. There was a suggestion that several species may

have shown seasonal changes or shifts in utilization of different container types, but there were insufficient data to test that possibility. *Aedes aegypti* gradually declined in frequency over the course of the study. Although *aegypti* abundance appeared to be inversely related to environmental temperatures, island-wide studies by Moore *et al.* (1978) indicate that this is not the case. *Culex secutor* abundance was highly correlated with rainfall (Kendall rank correlation coefficient, τ = 0.71, P = 0.001), with a lag effect of about 15 days.

Discussion

There was no evidence of behavioral change in *Aedes aegypti* populations in western Puerto Rico as a result of the *Aedes aegypti* Eradication Program. Over 99% of all positive collections were made at distances of less than 85 meters from the nearest house, and no *Ae. aegypti* were found more than 100 m from houses. Similarly, natural container breeding sites made up only 17% of the total. Reports of unusual behavior (Fox *et al.,* 1960; Weinbren and Weinbren, 1970) were shown to be due to spillover from nearby domestic breeding sites or to transitory establishment following introduction of *Ae. aegypti* into an isolated focus of intense human activity (Haber and Moore, 1973).

Whenever *Aedes aegypti* has been introduced into new regions of the tropics, it has tended to displace the indigenous container-breeding *Aedes* of that region (Bailey and Bohart, 1952; Macdonald, 1956; Gilotra *et al.,* 1967; Chan *et al.,* 1971). Laboratory studies have similarly demonstrated the ability of *Ae. aegypti* to exclude other *Aedes* species (Wilton, 1968; Moore and Fisher, 1969; Peters *et al.,* 1969).

Aedes aegypti was probably introduced into Puerto Rico soon after the arrival of slaves from Africa in the early 16th century (Picó, 1969). Thus, *Ae. aegypti* has had more than 400 years and perhaps 5000 to 13,000 generations in which to evolve an optimal division of the container environment with local species.

The highly negative association between *Ae. aegypti* and the other major container-breeding species suggests that, if competitive displacement occurred, it did so some time ago. There appear to be major differences in oviposition sites (e.g., shade, organic content, pH), not measured in this study, that influence gravid females in selecting containers not attractive to *Ae. aegypti.* Conversely, *Ae. aegypti* seems able to utilize certain container habitats more effectively than can other species. This appears to be an example of an "included niche" (Schoener, 1974), as the other species have a broader niche than *Ae. aegypti* (either on the container type or distance axes, or both).

Additional studies are needed to clearly define the parameters that reduce or prevent competition among container-breeding mosquitoes. Some parameters that should be included in future studies are shade, height, density and species of surrounding vegetation; organic content (quality and quantity), pH, salinity, and source (rain or human activity) of the water; and orientation of the container. Future studies should also be carried on long enough to demonstrate any seasonal separation between species.

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